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Original Article

Collective action and the intensity of between-group competition in nonhuman primates

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The importance of between-group competition in the social evolution of animal societies is controversial, particularly with respect to understanding the origins and maintenance of cooperation in our own species. Among primates, aggressive between-group encounters are often rare or strikingly absent, a phenomenon that in some species has been ascribed to the presence of collective action problems. Here, we report on a series of comparative tests that show that the intensity of between-group contest competition is indeed lower in species that experience a collective action problem while controlling for predictions from an "ideal gas" model of animal encounters and general species' ecology. Species that do not succumb to the collective action problem are either cooperative breeders, are characterized by philopatry of the dominant sex, or live in relatively small groups with few individuals of this dominant sex. This implies that collective action problems are averted either through shared genes and benefits or a by-product mutualism in which the territorial behavior of some privileged individuals is not affected by the behavior of others. We conclude that across the primate taxon, the intensity of between-group competition is predominantly constrained by a social dilemma among group members, rather than ecological conditions, and that the collective action problem is thus an important selective pressure in the evolution of primate (including human) cooperation and sociality.

Key words: **collective action problem, competition, cooperation, ideal gas model, social evolution, territoriality.**

INTRODUCTION

Although the causes and consequences of competition among individual organisms are generally well understood, controversy reigns over its evolutionary significance at the level of groups (West et al. 2007; Wilson and Wilson 2007), where effective competition typically requires cooperation among individuals. Thus, although some have seen increased competitive ability of the collective as the root cause of group-living and social bonds among animals (Wrangham 1980), others have argued that between-group competition at best plays a secondary role (Alexander 1974; van Schaik 1996). A series of high-profile publications recently rekindled this debate by suggesting that intense group selection is responsible for human warfare and, thereby, has played a crucial role in the evolution of some of the unique aspects of human cooperation (Choi and Bowles 2007; Bowles 2009, 2012), a suggestion challenged by others (Langergraber et al. 2011; Tomasello et al. 2012; Fry and Söderberg 2013).

In highly social species, ranging from ants (Wilson 1971) to humans (Keeley 1996), individuals engage in escalated collective aggression against conspecifics, sometimes with lethal consequences. According to socioecological theory, such behavior can only evolve if the contested resources are economically defendable (Brown 1964; Davies and Houston 1984), which in social taxa is directly related to the group's collective competitive ability, or resource holding potential (Hölldobler and Lumsden 1980). In many group-living animals, effective collective action is readily achieved and a group's resource holding potential is simply a monotonically increasing function of group size (Hölldobler 1981; Mosser and Packer 2009). Among vertebrates, this is typically (though not exclusively) true for species that live in cooperatively breeding societies in which the selfish interests of group members are highly aligned, either through shared genes (i.e., kin selection: Hamilton 1964), shared benefits (e.g., group augmentation: Kokko et al. 2001; Kingma et al. 2014), or both (Clutton-Brock 2002). In other species, however, the competitive ability of a group is often undermined by the collective action problem (CAP: Olson 1965), which emerges whenever collective action creates a public good (e.g., a territory) and the selfish interests of group members are

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not highly aligned. In this scenario, natural selection will favor free riders over cooperators, as these reap the benefits of access to the good without incurring (their fair share of) the costs of producing it (Hawkes 1992; Nunn and Lewis 2001), thereby subverting group-level cooperation. Thus, even where ecological conditions are such that effective group territoriality would be in each individual's interest, CAPs may still prevent its manifestation.

Although CAPs have been described in other group-territorial species (Heinsohn and Packer 1995; Bonanni et al. 2010), they appear to be particularly prevalent across the primate taxon (van Schaik 1996; Nunn 2000; Kitchen and Beehner 2007; Willems et al. 2013) and were indeed first described in human societies (Olson 1965). Studies of several nonhuman primate species have shown that CAPs occur in both the context of territorial advertisement (Kitchen 2004) and defense against intrusions (Nunn and Deaner 2004; Harris 2010; Crofoot and Gilby 2012), but whether the emergence of such CAPs also affects the intensity of between-group contest experienced by different species remains an open question.

In this study, we systematically investigate whether CAPs influence the intensity of between-group competition across the primate taxon through a comparative analysis of a sample of 138 group-living species. This phylogenetic approach provides an alternative, yet complementary view to previous work on animal conflict and cooperation, which has overwhelmingly focused on within-species comparisons of the behavioral strategies of different individuals. Our study, in contrast, takes a macroevolutionary perspective and is concerned with detecting species-level patterns of correlated evolution between the intensity of between-group competition and effective within-group cooperation. We operationally define the intensity of between-group contest competition in each species as the number of aggressive between-group encounters that a modal group experiences per day and the potential presence of CAPs as the absence of spontaneous and contagious long-distance vocalizations used to advertise territoriality (cf. Nunn 2000).

First, we validate our behavioral proxy for the presence of CAPs by performing a series of phylogenetic comparisons between the socioecology of species that vocally advertise territoriality and those that do not. Both classic socioecological theory on territory economics and the CAP hypothesis predict that advertising species are more territorial and thus occupy ranges that overlap less. However, socioecological theory further expects advertising species to live in ranges that are more economically defendable (Brown 1964) and to exploit resources that provide a greater incentive to defend (Milinski and Parker 1991). In contrast, the CAP hypothesis focuses on the distribution of benefits among group members and predicts that territorial advertisement occurs in species in which it either 1) confers inclusive and/or mutualistic fitness benefits, as is the case in cooperatively breeding taxa (Clutton-Brock 2002) and species in which the dominant sex is philopatric (Willems et al. 2013), or 2) is sustained through by-product benefits and mutualisms in which the benefits are highly asymmetrically distributed among group members, so that the selfish territorial behavior of dominants (or "privileged individuals": Nunn 2000) is impervious to free riding by subordinates (Gavrilets and Fortunato 2014). This "exploitation of the great by the small" is most pronounced in small groups (Olson 1965) and priority-of-access models indeed confirm that the required (dominance-driven) skew in the distribution of benefits decreases with group size (Pandit and van Schaik 2003). Moreover, given that the territorial behaviors of group-living primates usually reflect the interest of the larger, more dominant sex (Cheney 1987; Willems et al. 2013), the CAP hypothesis also predicts that advertising species live in relatively small groups with few individuals of the dominant sex.

Second, having validated our behavioral proxy for the presence of territorial CAPs, we next assess whether the presence of a CAP reduces the intensity of between-group contest competition across species, given that free riders undermine the expression of territorial behavior. We thus hypothesize that the rate of aggressive between-group encounters in advertising species is higher than in species that do not advertise. However, we need to control this analysis for predictions from the "ideal gas" model, a well-established null-model of animal encounter rates (Waser 1976; Hutchinson and Waser 2007). This model, derived from the kinetic theory of gases, postulates that the collision rate among particles increases with their size, relative mobility, and density. In biological terms, this translates into the null-expectation that between-group encounter rates increase with 1) group spread or size, 2) average daily travel distance relative to the home range area, and 3) the degree of home range overlap or population density (Hutchinson and Waser 2007). In addition, we simultaneously investigate potential differences in encounter rates due to general aspects of species' ecology and correct for phylogenetic nonindependence.

MATERIAL AND METHODS

Data collection

We collected information from the literature on the occurrence of territorial advertisement (yes/no), rates of aggressive between-group encounters (*n*/daily activity period), home range overlap (as a proportion of the total range), group size and composition (total number of individuals and the number of adult males and females), day journey length (km), home range size (km^2), and dietary composition from more than 200 natural primate populations, representing a total of 138 group-living species. Note that our definition of territorial advertisement as "the presence of spontaneous and contagious long-distance vocalizations between social groups, often in the form of dawn choruses prior to group movement" (Marler 1968), was slightly more restrictive than the one used in 2 previous studies on primate long-distance vocalizations (Nunn 2000; Wich and Nunn 2002): in order to ensure that we scored only those long-distance vocalizations that serve as active (i.e., not in response to the perceived presence of, or previous interaction with neighboring groups) signals in between-group communication, we additionally required a consensus among authors in the taxon-specific literature on such calls primarily functioning in the context of territorial advertisement. The absence of vocal territorial advertisement in a species has previously been taken to signify the presence of a CAP among members of the calling sex in the coordination of territorial behavior (Nunn 2000). Our first set of analyses sets out to validate this interpretation, before we adopt it in our second set of analyses to investigate whether territorial CAPs affect the intensity of between-group competition across species.

Intensity of between-group contest competition was expressed as the average number of aggressive encounters that the modal group of a species experienced per day. For an encounter to qualify as aggressive, it had to minimally exhibit one of the following behaviors among individuals of opposing groups: either an exchange at close proximity (depending on species, up to 50 m) of agonistic facial expressions and vocalizations (other than the long-distance territorial advertisement call) or agonistic physical interactions such

as chases, pushes, hits, or bites. Our rationale is thus that potential fitness costs of between-group competition will tend to increase across the primate taxon with the frequency of aggressive encounters between adjacent mixed-sex groups (Cheney 1992).

Information on day journey length and home range size was used to calculate the mobility of groups within their ranging areas, which in nonvolant species equates to the economic defendability of the home range, or *D*-index (Mitani and Rodman 1979). This *D*-index quantifies the ability to effectively monitor range boundaries and is specified as the ratio of the average daily path length and the diameter of the (idealized) ranging area. As such, the *D*-index is indifferent to whether exclusive access to the ranging area itself (i.e., space) or the critical resources therein (the spatiotemporally varying distribution and abundance of food, shelter, or mating opportunities) is defended, which makes it a particularly suited and general index to assess the economic feasibility of any form of territorial defense. Moreover, to gauge the ecological incentive animals may have to defend a territory, we looked at the dietary composition of focal groups, expressed as the proportion of leaves in their diet. As the degree of folivory (and thereby the abundance and homogeneity of resource distribution) increases, we assume that the incentive for ecological resource defense decreases (Milinski and Parker 1991).

Only data from studies on free-ranging, nonprovisioned groups were considered, and in addition, we scored the following characteristics at the species level from reviews by Smuts et al. (1987), Campbell et al. (2011), and the "All the World's Primates" online database (Rowe and Myers 2014): activity period (diurnal or nocturnal/cathemeral), habitat type (open or wooded), and substrate use (arboreal or—at least to some extent—terrestrial). For species in our sample represented by multiple populations, we calculated averages/medians for continuous/discrete variables, respectively. Additional details can be found in the Supplementary Material.

Statistical analyses

To correct for nonindependence among species, we used phylogenetic generalized least-squared models (PGLS) for continuous response variables (Freckleton et al. 2002) and generalized estimating equations based on phylogenetically corrected degrees of freedom (comparative GEE) for binomial species' traits (Paradis and Claude 2002). A variance covariance matrix was calculated using a Bayesian consensus tree obtained from the 10K Trees Project (version 3; Arnold et al. 2010), extended following van Woerden et al. (2012), and incorporated into all statistical analyses to model phylogenetic dependency. Where required, response and predictor variables were transformed prior to analysis. All analyses were conducted in R version 3.0.1 (R Core Team 2014) using the "caper" (Orme et al. 2012) and "ape" packages (Paradis et al. 2004).

RESULTS

In our sample of 138 group-living primate species, approximately 45% (n = 62) was reported not to use contagious and spontaneous long-distance vocalizations to advertise territoriality (Supplementary Figure S1), potentially signifying the presence of territorial CAPs. Conversely, in some 55% of species, including all cooperative breeders in our sample (n = 21, or 15% of the total), long-distance territorial vocalizations were present.

To validate the absence of territorial advertisement as a behavioral correlate of the presence of CAPs, we first investigated the socioecological differences between advertising and nonadvertising species. Advertising species were found to have home ranges that overlap less (mean ± standard error of the mean [SEM] = 25.0% ± 2.74) than those of nonadvertising species (mean ± SEM = 54.3% ± 4.00; PGLS: $\lambda_{ML} = 0.707$; $R^2_{Adj.} = 0.166$, $F_{1,133} = 27.58$, $P < 0.0001$; Figure 1), confirming their more effective range defense. However, advertisers did not differ from nonadvertisers in the economic defendability of home ranges (mean ± SEM = 1.72 ± 0.16 vs. 1.36 ± 0.14, respectively; PGLS: $\lambda_{ML} = 0.900$; $R^2_{Adj.} = 0.007$, $F_{1,125} = 0.068$, $P = 0.79$), nor in their degree of folivory (mean ± SEM = 0.31 ± 0.03 vs. 0.26 ± 0.03; PGLS: $\lambda_{ML} = 0.941$; $R^2_{Adj.} = 0.008$, $F_{1,129} = 0.01$, $P = 0.94$), contrary to expectations from classic socioecological theory. On the other hand, advertising species did live in smaller groups (mean ± SEM = 8.07 ± 0.68 vs. 39.5 ± 6.1; PGLS: $\lambda_{ML} = 0.956$; $R^2_{Adj.} = 0.099$, $F_{1,134} = 15.89$, $P < 0.0005$) with fewer individuals of the larger sex (mean ± SEM = 1.60 ± 0.11 vs. 5.15 ± 0.77; PGLS: $\lambda_{ML} = 0.916$; $R^2_{Adj.} = 0.067$, $F_{1,132} = 10.65$, $P < 0.005$), consistent with predictions from the CAP hypothesis. No significant differences could be ascribed to general species' ecology: activity period (comparative GEE: $F_{1,16.08} < 0.001$, $P = 0.99$), preferred habitat type (comparative GEE: $F_{1,16.08} = 2.10$, $P = 0.17$), or substrate use (comparative GEE: $F_{1,16.08} = 0.681$, $P = 0.42$).

It might be objected that these comparisons do not separate true collective territorial defense from private actions by a single partner in pair-living species or single males in polygynous groups. To exclude public good production (i.e., the effective defense of space, food, shelter, or mating opportunities) as a mere by-product of such selfish, noncollective behaviors by single individuals, we repeated all analyses using a subset of the data that only comprised species in which the modal group contains multiple individuals of the dominant, larger sex (males in 68, and females in 4 out of 72 species) and in which, at least on some occasions, more than one of these individuals are simultaneously involved in aggressive between-group encounters. These analyses corroborated all previous results (Supplementary Figure S2), thereby underscoring that CAPs become more acute as the number of individuals of the dominant sex in the modal group increases rather than simply arise when more than a single individual of this sex is present. Overall then, findings from this first set of analyses provide compelling support for the interpretation of the absence of territorial advertisement as evidence for the presence of a CAP (Nunn 2000) rather than being due to any ecological constraints.

Our second set of analyses thus proceeded to use territorial advertisement as a behavioral proxy to investigate whether the CAP affects the intensity of between-group competition across species. A PGLS analysis ($\lambda_{ML} = 0.000$; $R^2_{Adj.} = 0.288$, $F_{9,69} = 4.50$, $P < 0.0005$; Table 1) confirmed the predicted effect of territorial advertisement ($t = 4.74$, $P < 0.0001$), with the rate of aggressive encounters being more than 60% higher in advertising (mean ± standard error [SE] = 0.255 ± 0.04 encounters/day) than nonadvertising species (mean ± SE = 0.153 ± 0.03 encounters/day). At the same time, the rate of aggressive between-group encounters also followed predictions from the "ideal gas" model, albeit in a subtly different way in arboreal and terrestrial species (Table 1). In all species, the rate of aggressive encounters increased with group size, relative mobility ($t = 3.25$, $P < 0.005$), and home range overlap ($t = 4.12$, $P < 0.0005$), where the positive effect of group size was less pronounced in terrestrial than arboreal species ($t = -2.29$, $P < 0.05$). No significant influence of other general species' traits was detected.

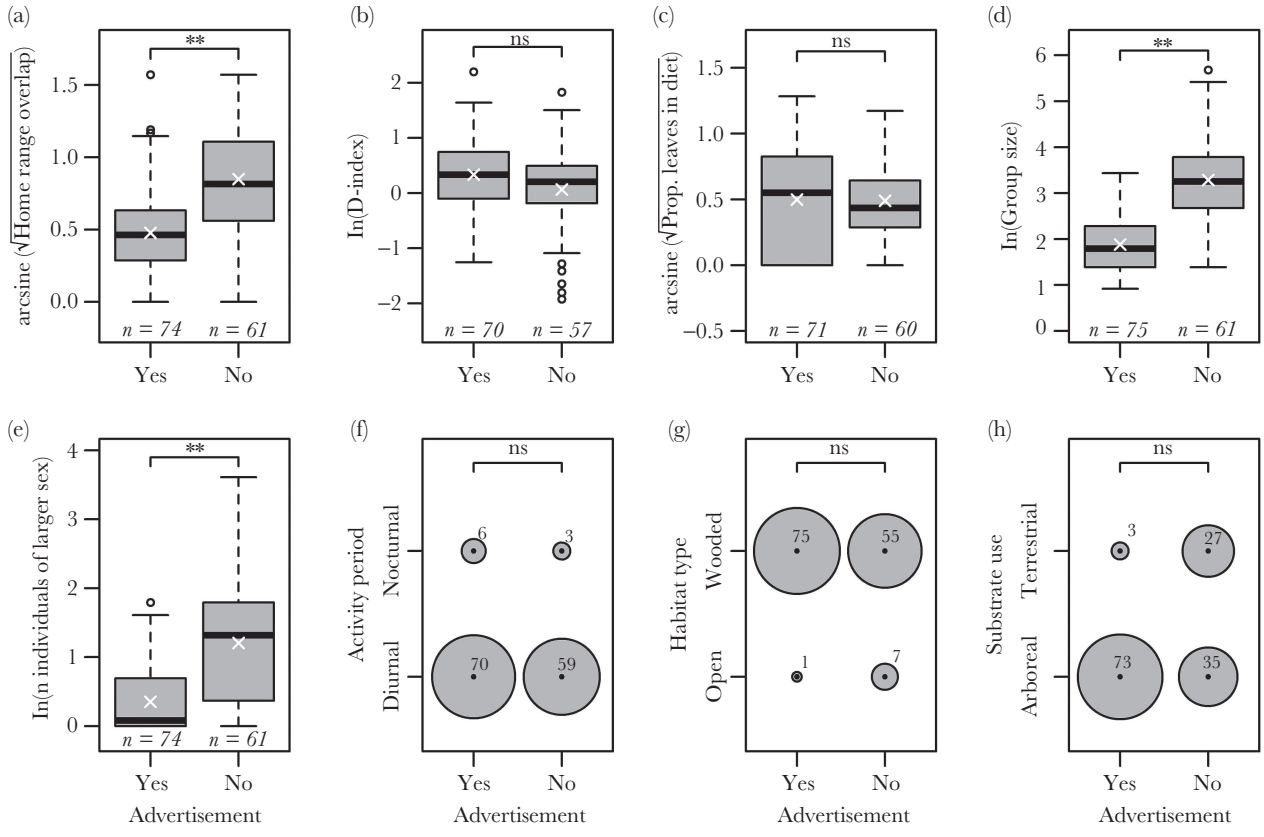

Figure 1

Phylogenetic comparisons to investigate the socioecological differences between advertising and nonadvertising species. Advertising species have lower levels of home range overlap (a) and live in smaller groups (d) with fewer individuals of the larger, dominant sex (e). No differences in economic defendability (b), ecological incentive (c), or general species ecology (f–h) were apparent. This pattern is in line with expectations from the CAP hypothesis and validates Nunn's (2000) previous suggestion that the absence of territorial advertisement can be interpreted as a behavioral proxy for the presence of a territorial CAP. ns: nonsignificant. **Significant at $\alpha = 0.00625$ (Bonferroni corrected).

Table 1

The rate of aggressive between-group encounters in all species in our sample for which data on all predictor variables were available ($n = 79$)

Variable	*B*	SE	*t* value	*P*
Intercept	−0.121	0.11		
Group territorial				
Advertisement	0.249	0.05	4.74	**0.0001**
Ideal gas model				
Group size	0.098	0.03	3.04	0.0033
Mobility (*D*-index)	0.105	0.03	3.25	**0.0018**
Overlap	0.210	0.05	4.12	**0.0001**
Species ecology				
Diet	−0.045	0.05	−0.84	0.4018
Activity period	−0.110	0.11	−1.00	0.3225
Habitat type	0.042	0.08	0.54	0.5882
Substrate use	0.650	0.27	2.39	0.0120
Interaction group size x substrate use				
Group size × arboreal	—	—	—	—
Group size × terrestrial	−0.181	0.08	−2.29	**0.0253**

In line with predictions from the CAP hypothesis and the "ideal gas" model of animal encounters, the rate of aggressive between-group encounters is higher in advertising species while simultaneously increasing with group size, relative mobility, and home range overlap. Moreover, compared with arboreal species, the rate of aggressive encounters in terrestrial species increases less steeply with group size. Significant highest-order effects are highlighted in bold. $\lambda_{ML} = 0.000$; $R^2_{Adj.} = 0.288$, $F_{9,69} = 4.50$, $P < 0.0005$.

As in our first set of analyses, we repeated the second analysis using only those species in which the modal group contains multiple individuals of the larger sex that are, at least occasionally, simultaneously involved in aggressive between-group encounters. This served to exclude species in which territorial defense reflects the selfish, noncollective behaviors of single individuals. Note that because all of the retained species ($n = 39$) were diurnal, we no longer included activity period as a predictor variable. Results from this follow-up analysis (Supplementary Table S1) substantiated all findings from the model based on all species. Our second set of analyses thus unequivocally shows that the rate of aggressive between-group encounters is lower in species in which a CAP among individuals of the larger sex occurs than in species in which it is absent (or overcome).

DISCUSSION

This study has demonstrated that the intensity of between-group competition in social primates is strongly affected by the presence of territorial CAPs. Because there is no reason to think primates unique among animals living in stable mixed-sex groups, our findings readily extend to other social taxa and may also have important repercussions for current debates on the evolutionary origins of human warfare (defined as collective between-group aggression) and altruism.

First, in evaluating a behavioral proxy for the presence of CAPs in primate territorial behavior (i.e., the absence of vocal territorial advertisement: Nunn 2000), we found that species in which

(collective) territorial advertisement occurs exhibit more effective group territoriality than species in which it does not, indicated by less home range overlap (Figure 1a), irrespective of ecological constraints such as economic defendability (Figure 1b) or ecological incentive (Figure 1c) and in line with the CAP hypothesis. Crucially, species in which territorial defense is more effectively maintained, either live in groups with a single representative of the dominant sex (in which the public good of territorial defense is produced as a by-product of selfish, noncollective behaviors), are cooperative breeders, or live in smaller groups (Figure 1d) that contain fewer individuals of the dominant sex (Figure 1e) than species in which collective defense breaks down. These results were obtained while controlling for potentially confounding effects of general species' ecology and phylogeny and are conceptually summarized in Table 2. We emphasize that, although we did not find any evidence for an influence of ecological constraints on primate territoriality between species, this does not exclude the possibility that local ecology affects the expression of territorial behaviors within species. Similarly, our findings do not imply that economic defendability of resources is not a necessary condition for the evolution and maintenance of territoriality, but merely that in and of itself, it is not a sufficient condition (see also Mitani and Rodman 1979).

Second, while controlling for predictions from an "ideal gas" model on expected encounter rates, we established that the rate of aggressive between-group encounters was more than 60% higher in species that do not experience CAPs (or in which they are overcome) than in species that do (Table 1). Interestingly, we also found that when contrasted against arboreal species, the rate of aggressive encounters in terrestrial taxa increased relatively less steeply with group size. This most plausibly reflects the fact that arboreal species live in much smaller groups than terrestrial species (median = 8.00 vs. 38.38, respectively), such that an equal absolute increase in group size, will have a relatively larger impact on the probability of encountering neighboring groups in the former than in the latter. Taken together, our findings indicate that the intensity of between-group competition in primates is more strongly affected by social dilemmas rather than ecological conditions and that the CAP is an important selective force in the social evolution of all group-living primates.

Overall, we found evidence for the presence of CAPs in 45% of species in our sample, representing all major radiations of social primates (Lemuriformes, Platyrrhini, and Catarrhini). A distinct and anticipated exception to this prevalence of CAPs in primate territoriality are cooperatively breeding species (but note that removing these taxa from our main analysis did not change its results; Supplementary Table S2). In line with evidence from other cooperatively breeding vertebrates (Clutton-Brock 2002), CAPs did not affect territoriality in any of the cooperatively breeding species in our sample. This finding, nevertheless, should not be taken to suggest that more subtle forms of free riding cannot exist in these species: "weak free riders" do not necessarily undermine the production of a public good but may still procure more than their fair share of the benefits (Heinsohn and Packer 1995; Nunn and Lewis 2001). The effects of weak free riding, however, are beyond the grain of analysis of a broad comparative study as the one presented here and would require intraspecific comparisons or dedicated experimental work on a focal population or group.

We acknowledge that the behavioral proxy we used for the presence of CAPs is not perfect. First, the occurrence of vocal territorial advertisement in a species does not always equate to the absence of CAPs in cooperative defense. In certain taxa, the larger, advertising sex (typically males) is represented by 1 individual only, and CAPs in the context of territorial advertisement can thus not occur. Yet, during territorial disputes over ecological resources such as space, food, or shelter, the smaller sex (typically females) may actually be the more actively involved sex, so that CAPs in the joint defense aspect of territoriality can still emerge. It is thus important to point out that our

Table 2

Conceptual summary of the main findings of this study to account for the incidence of group-territorial behaviors across the primate taxon

	Group territoriality	
	No	Yes
Territory economics	**Undefended home range is ESS** –Economic defendability: not possible to defend (low *D*-index) and/or –Resource abundance and distribution: no incentive to defend (high folivory)	**Defended territory is ESS** –Economic defendability: possible to defend (high *D*-index) and –Resource abundance and distribution: strong incentive to defend (low folivory)
	CAP	
No	**Not expected** Not observed	**a. By-product benefit** Groups with only 1 individual of dominant sex –No group-level cooperation required **b. Indirect benefit (kin selection)** Cooperative breeders/philopatry dominant sex –Individuals highly related **c. Direct benefit (e.g., group augmentation)** Cooperative breeders –Individual interests highly aligned
Yes	**Suboptimal territorial defense** Large groups, many individuals dominant sex –Low skew in the distribution of benefits, public good (i.e., territory) is not produced	**By-product benefit** Small groups, few individuals of dominant sex –High skew in the distribution of benefits, set of "privileged individuals" produces public good out of selfish interest

Our analyses did not generate support for classic territory economics theory based on ecological constraints. Instead, we found overwhelming support for the view that effective group territoriality provides a public good, the production of which is prone to the CAP yet can be maintained by either by-product, indirect, or direct fitness benefits to individuals. ESS: evolutionarily stable strategy.

proxy can only inform about the potential presence of CAPs among individuals of the larger, advertising sex. Second, our proxy implicitly assumes that, in principle, long-distance vocalizations can occur in all species. Indeed, although long-distance vocalizations are considered the ancestral state in primates (Wich and Nunn 2002), not a single species in our sample with high fission–fusion dynamics ($n = 13$) was reported to primarily use such calls in the context of between-group communication. Nevertheless, 6 of these taxa (*Pan troglodytes* subspp., *Ateles* spp., and *Brachyteles arachnoides*) are known to be highly group territorial and are thought to avert potential CAPs through the indirect and/or direct fitness benefits conferred by male philopatry and bonding (Widdig 2013; Willems et al. 2013). If anything, this implies that our proxy could have resulted in overly conservative conclusions about the significance of CAPs in primate territoriality. Removing all fission–fusion species from our analyses, however, corroborated all results and conclusions obtained from the full data set (Supplementary Table S3). Despite these limitations (which are almost inherent to any broad phylogenetic comparison based on behavioral data), our first set of analyses overwhelmingly vindicates the previously suggested interpretation of the presence of territorial advertisement as a biologically informative correlate of the absence of territorial CAPs (Nunn 2000).

Our findings show that territorial CAPs among group members considerably decrease the intensity of between-group competition, strongly suggesting that between-group competition may not be a universally important selective force in the evolution of primate sociality and cooperation (see also Crofoot and Gilby 2012). Viewed in a multilevel selection framework (Wilson and Wilson 2007), we thus observe that within-group, rather than between-group, competition appears to be the dominant selective force in social primates: in fact, our study reveals that intense within-group competition, of which the CAP is only one of many possible manifestations, erodes the significance of group-level selection by undermining effective group-level cooperation. As such, our findings are inconsistent with an influential model of primate sociality that postulates that individuals in larger groups enjoy a categorical advantage over individuals in smaller groups during between-group competition situations (Wrangham 1980). The data, in contrast, reveal that collective territoriality is more effectively maintained in species that live in smaller groups that contain fewer individuals of the larger, more actively involved, sex (apart from cooperatively breeding and male bonded fission–fusion species). These results, moreover, may shed light on the evolution of escalated between-group competition and aggression in humans, that is, warfare (Keeley 1996). The only nonmonogamous, group-living primates in which individuals of the larger sex are able to mount effective collective territorial action are either cooperative breeders or, if living in large fission–fusion groups, male bonded species. In any species where these 2 features co-occur, we should therefore expect pronounced collective territoriality. Indeed, among primates, this is uniquely the case in humans (Blaffer-Hrdy 2009; Hill and Hurtado 2009), and we therefore conclude that it is more parsimonious to view the highly cooperative nature of human societies as an evolutionary precondition for warfare (Langergraber et al. 2011; Tomasello et al. 2012; Fry and Söderberg 2013) rather than as a consequence of intense group-level selection (contra: Choi and Bowles 2007; Bowles 2009, 2012).

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/

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